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BOTRYTIS NECK ROTS OF ONIONS [1]

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INTRODUCTION

The serious nature of losses due to Botrytis infection of onion bulbs first came to the writer's attention in the late autumn of 1915. During the subsequent winter the damage from this malady in midwestern onion-growing districts was of such magnitude as to leave no doubt as to its importance. Investigations were begun in 1917 upon the nature and causes of the disease and possible remedial measures. About the time this work was started, Munn (*20*)[2] published his report in which the cause of neck rot of onion was attributed to *Botrytis allii* Munn. His findings, in so far as they relate to the cause of the disease, have in the main been confirmed. In addition it has been found that a second species, *B. byssoidea* Walker is the more common cause of neck rot in Wisconsin and Illinois sections, and that a third species, *B. squamosa* Walker also causes a neck-rot decay (*34*).

It is the purpose of the present paper to review briefly the history of neck rot as so far treated in the literature, and to report studies upon the three forms of neck rot which are now known to occur. Since each of these three forms produces distinct symptoms and is caused by a distinct species of Botrytis, the three maladies must in any critical consideration be regarded as separate diseases. On the other hand, their similarity in so many respects is justification for referring to them by a group name which will indicate that they are similar diseases caused by closely related organisms. There are several reasons for allowing the term "onion neck rot" to apply to the group. It is an accurate and adequate common term already in good usage; it was probably applied to one or all of the three diseases before any clear differentiation was made; and all three parasites invade the onion bulb chiefly through the neck tissues.

For differentiating between the three types of neck rot it has been suggested that descriptive adjectives be used (*34*). For the form already described by Munn (*20*) as due to *Botrytis allii*, the term "gray-mold neck rot" is used because of the prompt and abundant production of gray conidial masses upon the decaying host tissue. For the second form, due to *B. byssoidea*, the name "mycelial neck rot" is suggested because of the predominance of mycelium and the

[1] Received for publication July 13, 1926; issued December, 1926.

[2] Reference is made by number (italic) to "Literature cited," p. 926.

scarcity of conidia on the decayed host tissue, as compared with the previous form. For the third form, due to *B. squamosa*, the name "small sclerotial neck rot" is suggested because the appearance of small sclerotia upon affected scales (i. e., small as compared with those of the other two forms) is an early and fairly constant sign of the disease.

HISTORY AND DISTRIBUTION OF ONION NECK-ROT DISEASES

The first description of onion neck rot was apparently that by Sorauer in Germany in 1876 (*25*). He again described it in the second edition of his textbook, in 1886 (*26, p. 294–297*). The symptoms which he has recorded correspond closely with those later given by Munn (*20*). He considered the form of Botrytis causing the disease to be *Botrytis cana* (Pers.) Fr. and the sclerotia probably to be identical with those which had been previously described as *Sclerotium cepae* Berk. and Br. He inclined to the view that the latter would give rise to an ascigerous stage identical with *Sclerotinia fuckeliana* but did not adduce any evidence to substantiate this view. It is likely, considering the size of conidia which he reports, that the form he had under observation was identical with *B. allii* Munn. He was able to reproduce the disease by artificial inoculation of healthy bulbs with conidia, but noted that the success of such inoculations depended on the presence of humid conditions. The severity of the disease in the field was dependent to a marked degree upon the amount of humid weather which prevailed about harvest time, a factor which later workers have likewise found to be of great importance. He was unable to produce infection upon healthy, vigorous, green onion leaves. He noted the conspicuous varietal differences in susceptibility, which have been recorded many times since, namely, that the white type of onion is very susceptible, whereas the yellow and red types are much less seriously affected.

Frank (*8*) described the disease, also from Germany, in his textbook in 1880. He added little to the facts given by Sorauer except that he claimed to have produced infection upon the green leaves of onion by means of artificial inoculation. He considered the causal organism to be identical with *Botrytis cinerea* Fr. Smith (*24*) in 1900 discussed the onion neck-rot disease which he found at Munich, Germany, and pointed out that the organism was distinct from *B. cinerea* both with respect to the shape of conidia and with regard to the low, creeping growth of the fungus as it sporulated upon decaying onion tissue. He was most likely working with *B. allii*.

A neck-rot disease was first reported from England by Massee (*18*) in 1894. Though he attributed the cause to *Sclerotinia bulborum* Wakker, experimental proof of the causal relations is lacking. An illustration showing the disease, in a later publication (*19*), indicates that he was dealing with either *Botrytis allii* or *B. byssoidea*. Cotton and Owen (*7*) later reported the occurrence of *B. allii* in England.

In 1903 Voglino (*29*) distinguished the Botrytis disease of onion found in Italy from that caused by *Sclerotium cepivorum* Berk. and referred the neck-rot fungus to *S. ambiguum* Duby.

Hanzawa (*10*) in 1914 reported a Botrytis disease of onion bulbs in Japan. He gave the size of conidia as 8.4 to 16.8 by 6.3 to 10.5 μ and considered that it was probably identical with *Botrytis cinerea.* These measurements correspond most closely with those of *B. byssoidea,* but it is impossible to determine with certainty from his meager description whether the form he studied was *B. allii* or *B. byssoidea.*

Halsted (*9*), the first to record the disease in America, gave a brief report of its occurrence in New Jersey in 1890, and referred to the causal organism as *Botrytis parasitica* Cav. Clinton (*4, 5*) reported serious epiphytotics of neck rot upon white onions in Connecticut in 1902 and 1903. He reported that the fungus caused yellowish spots on the leaves of the onion plant in July and also blasted the flowers of the seed plant. He pointed out the importance of humid weather in bringing about heavy infection and attributed the absence of the disease in 1904 largely to the dry weather which prevailed during July and August of that year.

Selby (*23*), writing in 1910, considered this to be the most serious disease of white onions in Ohio. He erroneously identified the causal agent as *Sclerotium cepivorum.* This fungus, described originally by Berkeley (*1*), produces minute sclerotia, while the diseased specimens illustrated by Selby are characteristic of those produced by *Botrytis allii* and by *B. byssoidea.* Humbert (*13*), writing on the same disease from Ohio, also referred to the causal organism as *S. cepivorum,* but that this interpretation is erroneous is obvious from his description of conidia and his illustration of a diseased onion bulb, which is similar to that published by Selby.

A neck-rot disease of onion was destructive to onions in Oregon in 1912, according to Jackson (*14*), and from his description it is apparent that *Botrytis allii* was the chief causal agent in that case. Munn (*20*) found neck rot repeatedly in New York and Michigan from 1913 to 1916, and described the disease as caused by *B. allii.* The data accumulated by the Plant Disease Survey (*3, 6, 11, 15, 28*) from 1921 to 1925 are sufficient to show that onion neck rot is widespread in this country. Although more consistent losses are perhaps sustained in the North, most onion-growing areas suffer from time to time, while the damage in a given locality varies widely with the season.

In many of the references cited above it is hardly possible to distinguish between the three types of neck rot. In practically all of the instances noted it is quite evident that the causal organism was either *Botrytis allii* or *B. byssoidea. B. squamosa* seems heretofore to have attracted little attention. *B. allii* has been isolated by the writer from bulbs grown in California, midwestern States, Pennsylvania, and Connecticut, and Munn (*20*) obtained it from Michigan and New York bulbs. Moreover a culture isolated from onions in France and forwarded to the writer by the Centralstelle für Pilzkulturen at Baarn, Holland, under the name of *B. cana* was found to be identical with *B. allii.* The mycelial neck-rot form, *B. byssoidea,* has been isolated from bulbs grown in midwestern States and in Connecticut, and was found by the writer on onions in the market at Paris, France, in 1922. It would appear, therefore, to be quite as widespread in its occurrence as *B. allii.* The small sclerotial form, *B. squamosa*, has so far been isolated by the writer only from onions grown in the Middle West, but no extensive search has been made for it elsewhere.

BOTRYTIS AND SCLEROTIUM FORMS PREVIOUSLY DESCRIBED ON ALLIUM

The Botrytis and Sclerotium forms upon species of Allium which have been described in literature present a very confusing situation to the reader. Many of these are the result of collections made on dying or dead parts and may or may not have a connection with the neck-rot forms. One of the first sclerotial forms on *Allium cepa* to be described in Europe was *Sclerotium cepivorum* Berkeley (*1*). A recent survey has shown this to be widespread in Europe and to occur in America (*31*). There should be no cause for confusing it with the Botrytis forms on onion for it lacks conidia and has much smaller sclerotia, but nevertheless it has been confused with these forms by Sorauer (*26*), Bruck (*2*), Selby (*23*), and Humbert (*13*). Massee (*18*) refers to the form associated with neck rot as identical with *Sclerotinia bulborum* Wakker on hyacinths, but there seems to be no justification for his statement. Voglino's reference (*29*) of the Botrytis found on *Allium cepa* to *Sclerotium ambiguum* Duby seems unwarranted. The identity of the neck-rot Botrytis with *Botrytis cinerea* has been suggested by Frank (*8*) and Hanzawa (*10*), but the differentiation between the latter and the onion form from Germany with which he worked was pointed out by Smith (*24*), and the distinction between *B. cinerea* and *B. allii* was later made by Munn (*20*). There is no ground for considering either of the Botrytis forms on onion identical with *B. cana*, as suggested by Sorauer (*26*), with *B. aclada* Fres. (*21, v. 4, p. 131*), with *B. fulva* Link (*16, Abt. 8, p. 280–281*), or with *B. vulgaris* Fr. var. *interrupta* Fr. (*21, v. 4, p. 129*) the last three of which have been found on dead scales or stems of Allium. *B. parasitica* Cav., reported on *Allium ursinum* (*16, Abt. 8, p. 292*), and referred to by Halsted (*9*) as the cause of onion neck rot, has been studied recently by Hopkins (*12*) and is undoubtedly distinct from all the onion forms.

Saccardo (*21*) describes several species of Sclerotium which have been found on living or dead parts of various species of Allium. It is not likely that any of these forms are identical with either of the sclerotial forms associated with onion neck rot. *Sclerotium ambiguum* Duby, *S. inconspicuum* Lib., *S. pulveraceum* Dur. and Mont., and *S. sepivorum* Berk. (*21, v. 14, p. 1150–1151*) are all described as having very small sclerotia, smaller than those of *Botrytis squamosa*. A form producing thin, ovate-oblong, minute sclerotia, described as occurring on *Allium vineale*, suggests some similarity to *B. squamosa*, but this form was ascribed to *S. tulipae* Lib. var. *hyacinthi* Guep. (*21, v. 14, p. 1172*), which has been described fully by Hopkins (*12*) and presents no close similarity to the onion neck-rot forms. *S. brassicae* Pers. (*21, v. 14, p. 1164–1165*), and *S. durum* Pers. (*16, Abt. 9, p. 674–675*) are described as producing very large sclerotia. The former, found on *Allium victorialis*, yielded no Botrytis form, while the latter was said to produce a Botrytis stage identical with *B. cinerea*.

An undescribed species of yellow-spored form of Aspergillus was isolated from Italian-grown garlic by E. D. Eddy in 1919. This species was found by the writer to be pathogenic upon onion bulbs as well as upon garlic. It produces in the decayed bulb tissue dark brown to black, slightly elongate sclerotia 1 to 2 mm. in length, which might be confused with other forms. The yellow color of the spores and the brown cast of the sclerotia are the chief characters by which it is readily distinguished from the above-mentioned sclerotial forms on onion. The causal organism has been recently described as *Aspergillus alliaceus* Thom and Church (*27*).

Sclerotium rolfsii is sometimes found on bulbs of garlic, but as yet no occurrence on onion bulbs has come to the writer's attention. The sclerotia are readily distinguished from those of the above form by their decidedly lighter brown color.

Sawada (*22, p. 206–209*) has described a disease of *Allium cepa* and *Allium fistulosum* which occurs in Japan and Formosa. This is attributed to a newly described species, *Sclerotinia allii* Sawada. The malady is one which attacks the leaves and stems of the growing plant, however, and is not reported as a storage decay of bulbs. Sawada states that *Sclerotinia libertiana* Fuckl. (*Sclerotinia sclerotiorum* (Lib.) Massee) also attacks onion plants in Japan, but so far as the writer is aware this fungus has not been authentically described elsewhere as an onion pathogene.

GRAY-MOLD NECK ROT

SYMPTOMS

Gray-mold neck rot is found most commonly upon the bulbs after harvest, infection taking place most readily through the neck tissues. The first sign of the disease is the softening of the affected scale tissue, which takes on a sunken, cooked appearance characteristic of the advancing zone of the diseased areas. The margin between the diseased and healthy tissue is quite definite, and since the effect upon the host cells is produced somewhat in advance of the hyphae, usually little evidence of the fungus is visible there. As the mycelium multiplies in the older diseased area the affected tissue becomes grayish in color, and later a dense grayish mycelial mat often develops upon the surface of the scale. Under average conditions, conidial production is prompt. A dense layer of gray mold consisting of comparatively short conidiophores and myriads of conidia is produced on the outer diseased scales. The early production of spores, even under average room conditions, is characteristic of this form, whereas the other two forms are more tardy in sporulating.

The disease progresses most rapidly down the scales which have been originally infected in the neck, while the spread from one scale to another proceeds somewhat more slowly. In a cross section of a partially rotted bulb, at the advance margin of the disease, the parenchyma has a distinctly water-soaked appearance. A few millimeters above this point a grayish tinge and slight shrinkage in the decaying tissue become evident, while still farther up the shrinkage of the scales and the development of mycelium increase. On the outer scales conidial production is pronounced. Sclerotia occur in connection with the older decayed tissue, first as whitish mycelial masses, which become darker with age until they assume the appearance of hard, black, rounded, kernel-like bodies, spherical, oblong, or irregular, and varying from 1 to 3 mm. or more in length. They form usually on the outer surface of the scale or are slightly embedded in the diseased host tissue.

Occasionally infection takes place through the bases of onion scales or through wounds. The results—the progress of the disease and the appearance of the tissue—in such cases are quite similar to those in cases of neck infection. The older decayed bulb presents the appearance of a "mummy." While the host tissue in the beginning of its decay is somewhat watery, it desiccates rather promptly and does not give the appearance of being affected by common bacterial soft rot. The moisture which is released is often sufficient, however, to stimulate growth of the central bud, and the premature sprouting of affected bulbs is a common sign of the disease. Little or no offensive odor is occasioned by neck-rot decay. Commonly, however, soft-rot bacteria follow close upon *Botrytis allii*, in which case a more watery decay and more odor result. Certain phases of the disease are illustrated in Figure 1.

Botrytis allii, being a faculative saprophyte, develops commonly upon dead onion parts and other refuse in the field. Munn (*20*) reports finding it also upon the roots, leaves, and flower parts of the onion plant. It would appear from his experiments that the organism may act as a parasite upon the aerial parts of the growing plant. The writer has never found any of the three Botrytis forms attacking the actively growing parts of the plant. The older dying leaves and the tips of leaves turning yellow from other cause often show Botrytis conidial production during moist weather, but the actual initial damage caused by Botrytis is not ordinarily noticeable under midwestern conditions.

THE CAUSAL ORGANISM (BOTRYTIS ALLII)

The septate, branching mycelium of *Botrytis allii* has little in the way of distinctive characters. It is hyaline for the most part, sometimes taking on a slight tinge of color with age. The aerial hypae en masse have a smoky-gray cast, but only in the conidiophores do the walls take on a deep-brown color.

Appressoria, or holdfasts, are commonly formed by repeated branching of hyphae which comes into contact with the host surface or with the glass containers of pure cultures. The mycelium in these bodies for the most part contains denser cytoplasm than is found elsewhere, and the walls commonly are darkened in color, giving often a very dark macroscopic appearance to the holdfasts.

Sclerotia are commonly formed in or upon the decayed host tissue. The conditions which promote the formation of these resting bodies have not been worked out. It is not uncommon for an onion bulb to suffer complete decay without the production of sclerotia, but usually abundant sporulation takes place. Newly formed sclerotia appear as white, dense, velvety masses of mycelium, which soon darken somewhat. As development continues the surface assumes a waxy appearance, light brown at first, gradually becoming darker, until a hard, black, kernellike mass results. The mature sclerotia are variously shaped; they are rounded on the upper surface and are either flat or concavely depressed on the lower side when attached to the outer surface of the onion scale. They vary in size from 1 mm. or less to 4 or 5 mm., but most of them measure from 2 to 4 mm. It is not uncommon, however, to find many sclerotia aggregated into a crusty mass of considerable size. In

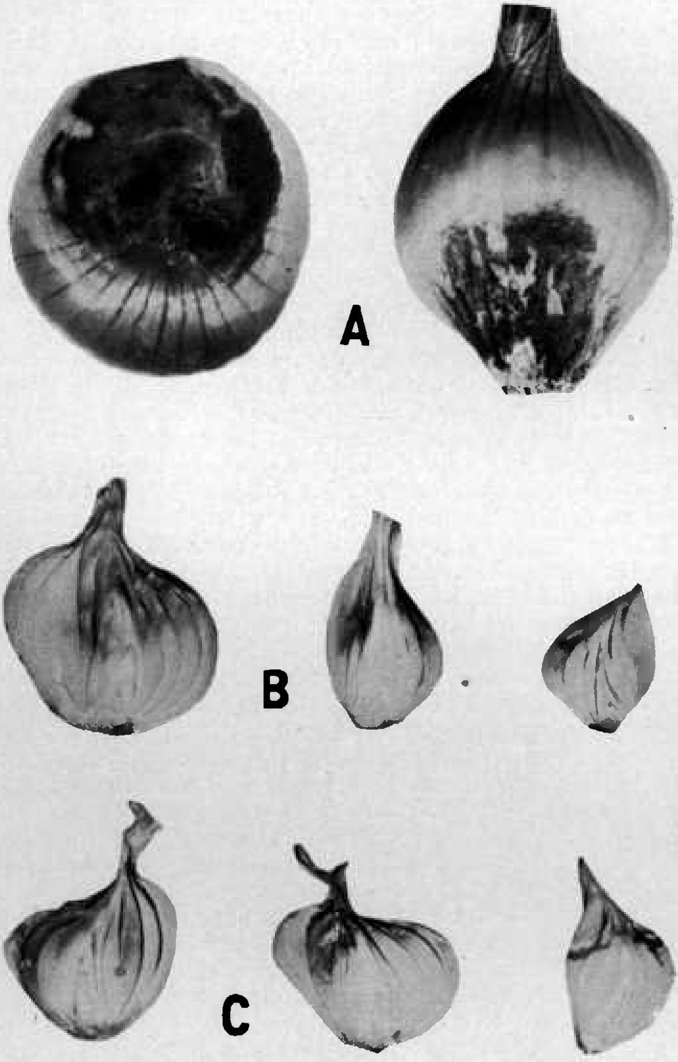

FIG. 1.—A, gray-mold neck rot (*Botrytis allii*). Natural infection. At left, Crystal Wax variety showing neck infection; at right, White Globe variety showing infection through base of bulb. Note characteristic gray mold on the decayed tissue. B, Crystal Wax bulbs inoculated with *Botrytis allii* through needle wounds, placed in moist chambers, and incubated (left to right) at 18°, 23°, and 26° C., respectively, for eight days. C, Crystal Wax bulbs inoculated with *Botrytis byssoidea* but handled otherwise like those in B. Note in B and C that the decay was most rapid at 18° C., somewhat less rapid at 23°, and very meager at 26°

cross section they exhibit a pseudoparenchymatous structure consisting of closely packed mycelial threads. The several outer layers consist of dark-walled cells which give the external black color to the bodies; the remaining interior is made up of hyaline cells. Under suitable conditions the sclerotia germinate either by sending out hyaline mycelial branches or by the direct production of conidiophores upon their surfaces.

The conidiophores are produced directly from the free mycelium in the tissues or from sclerotia. Branches are sent up approximately at right angles to the mycelial thread. (Fig. 6, A.) These are hyaline at first and remain so in the region of the growing tip, but the older portions of the conidiophore walls become gradually darker until they are a deep brown. They vary from 6 μ to 20 μ or more in diameter, are septate and occasionally branched, and usually attain a fairly uniform height above the surface of the host. With their profuse production of spores, they give a low, dense, gray-mold appearance, often distinguishable from the higher and less-compact habit of *Botrytis byssoidea.* The growing tip of the conidiophores preliminary to spore production sends out several side branches from the main stem and these rebranch once or twice. (Fig. 6, B.) The ends of these branches become rather swollen, and from these rounded tips the sterigmata which later produce the conidia are sent out in large numbers. (Fig. 6, C, D.) These sterigmata, after attaining a length of 1 μ to 2 μ, swell at their tips to form the spores. This takes place almost simultaneously on all the sporiferous tips. (Fig. 6, E.) While the spores are enlarging they are not readily detached from the conidiophore, but when they are mature they disperse readily when placed in liquid or when exposed to air currents. Cleavage of the spore usually takes place at the top of the sterigma, and the sterigma is not usually attached to the spore after dispersal. About the time of spore maturation, cross walls are laid down, first just behind the sporulating tips and finally in close proximity to the main stalk of the conidiophore. Degeneration begins above these septa, starting with the sterigmata and continuing with the sporiferous branches. (Fig. 6, F.)

The main branch of the conidiophore proliferates by extending upward (fig. 6, G), and in due time it again branches and repeats the process of sporulation. Each point of sporulation on the main stalk is marked by slight scars or knobs on the conidiophore where the septa were laid down to cut off the degenerating sporulating branches. (Fig. 6, H.) By this time the walls have usually become dark colored. The conidiophore may thus sporulate and proliferate several times during the course of its development, and the region of sporulation is marked each time by the group of scars where the branches were cut off, while the conidia remain grouped around these points if no liquid chances to come in contact with them or if they are not blown away by air currents. With age the conidiophore becomes flattened and twisted. Thus in nature it is not uncommon to find conidiophores 1 or 2 mm. in length with groups of spores adhering to them at regular intervals. Occasionally one of the sporulating branches does not degenerate but also proliferates and continues to sporulate, thus giving rise to the occasional branch found with the conidiophores of *Botrytis allii.*

In describing this phase of the morphology of the organism, Munn (*20*) does not mention the branching of the conidiophore previous to sporulation, and in describing and figuring the scars upon the main stalk he intimates that the conidia are produced directly upon them. It is not always easy to demonstrate the exact origin of the conidia, chiefly because the mature conidia disperse as soon as placed in water mount, but after repeated examination of the sporulating tips before the spores are mature and thus not readily detached, there is no reason to doubt that they are always formed in the manner just described.

The conidia are oblong to elliptical in shape, hyaline, and continuous. (Fig. 6, I.) They vary in size over a considerable range (6 to 16 by 4 to 8 μ), but measurement of a considerable number shows that a majority fall within the range of 7 to 11 by 5 to 6 μ. The frequency distribution of length and width for a number of strains growing on onion tissue and on potato agar, as given in Table 1, show a reasonable degree of constancy in range of size. By comparison with measurements of several strains of *Botrytis byssoidea* and of *B. squamosa* given in the same table, it is evident that *B. allii* falls in a class the average measurements of which are somewhat smaller than those of the other two species which affect onion bulbs. Germination takes place under favorable conditions in 12 to 14 hours by the production usually of a single germ tube, occasionally of two, and almost always without septation in the spore during germination. Microconidia are not common; they are globose, about 3 μ in diameter, and are borne on short hyaline conidiophores.

TABLE 1.—*Conidial measurements from a number of strains of Botrytis allii, B. byssoidea, and B. squamosa* [a]

Species	Strain No.	Source	Substrate	Percentage of spores falling within the length (in microns) of groups indicated																		
				6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Botrytis allii	64	Louisiana	Potato agar	--	10	32	34	16	6	2	--	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	--	12	36	44	8	--	--	--	--	--	--	--	--	--	--	--	--	--
	65	([b])	Potato agar	--	10	26	28	24	6	4	--	2	--	--	--	--	--	--	--	--	--	--
			Onion	--	2	16	36	36	10	--	--	--	--	--	--	--	--	--	--	--	--	--
	76	Illinois	Potato agar	2	10	14	14	22	10	14	4	4	2	4	--	--	--	--	--	--	--	--
			Onion	--	--	4	38	40	10	4	2	2	--	--	--	--	--	--	--	--	--	--
	77	do	Potato agar	--	8	14	22	30	16	2	4	4	--	--	--	--	--	--	--	--	--	--
	83	Ohio	do	--	12	22	24	28	10	2	2	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	--	18	56	20	6	--	--	--	--	--	--	--	--	--	--	--	--	--
	86	do	Potato agar	--	4	36	30	16	12	2	--	--	--	--	--	--	--	--	--	--	--	--
	88	Pennsylvania	do	2	20	24	26	20	4	2	2	--	--	--	--	--	--	--	--	--	--	--
	96	Illinois	Onion	--	--	--	32	40	20	4	4	--	--	--	--	--	--	--	--	--	--	--
	100	California	do	12	36	44	8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Botrytis byssoidea.	42	Wisconsin	do	--	--	2	2	4	2	12	12	30	22	2	8	2	2	--	--	--	--	--
	70	Illinois	do	--	--	--	--	2	6	10	28	28	14	4	2	6	--	--	--	--	--	--
	80	Wisconsin	do	--	--	--	--	4	12	26	14	20	12	2	4	2	2	2	--	--	--	--
	89	Illinois	Potato agar	--	--	--	2	30	22	20	20	6	--	--	--	--	--	--	--	--	--	--
			Onion	--	--	6	8	50	30	6	--	--	--	--	--	--	--	--	--	--	--	--
	90–1	do	Potato agar	--	--	--	6	30	44	16	2	0	0	2	--	--	--	--	--	--	--	--
	90–5	do	do	--	--	--	6	6	20	34	16	12	6	--	--	--	--	--	--	--	--	--
	90–7	do	do	--	--	--	2	10	16	26	16	14	6	8	2	--	--	--	--	--	--	--
	98	Wisconsin	Onion leaf	--	--	--	--	--	20	52	12	8	8	--	--	--	--	--	--	--	--	--
	101	do	do	--	--	--	--	4	36	16	44	--	--	--	--	--	--	--	--	--	--	--
	114	France	Onion	--	--	2	5	17	45	23	7	1	--	--	--	--	--	--	--	--	--	--
	94	Illinois	do	--	--	--	--	--	4	32	20	28	12	--	4	--	--	--	--	--	--	--
Botrytis squamosa.	27	Wisconsin	Potato agar	--	--	--	--	--	--	--	2	6	16	20	18	12	20	6	--	--	--	--
	30	do	do	--	--	--	--	--	--	--	--	2	--	8	6	8	22	18	18	12	6	--
	134	do	do	--	--	--	--	--	--	--	--	3	4	15	15	17	17	11	7	9	1	1

[a] In most cases 100 spores from each strain were measured.
[b] Culture No. 65 was furnished by M. T. Munn, New York State Agricultural Experiment Station.

TABLE 1.—*Conidial measurements from a number of strains of Botrytis allii, B. byssoidea, and B. squamosa*—Continued

Species	Strain No.	Source	Substrate	Percentage of spores falling within the width (in microns) of groups indicated														
				4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Botrytis allii	64	Louisiana	Potato agar	--	58	40	2	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	18	66	16	--	--	--	--	--	--	--	--	--	--	--
	65	(b)	Potato agar	2	88	10	--	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	6	42	42	10	--	--	--	--	--	--	--	--	--	--
	76	Illinois	Potato agar	4	68	26	2	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	18	60	20	2	--	--	--	--	--	--	--	--	--	--
	77	do	Potato agar	6	80	14	--	--	--	--	--	--	--	--	--	--	--	--
	83	Ohio	do	--	64	36	--	--	--	--	--	--	--	--	--	--	--	--
			Onion	--	38	60	2	--	--	--	--	--	--	--	--	--	--	--
	86	do	Potato agar	4	58	36	2	--	--	--	--	--	--	--	--	--	--	--
	88	Pennsylvania	do	--	62	38	--	--	--	--	--	--	--	--	--	--	--	--
	96	Illinois	Onion	--	24	68	8	--	--	--	--	--	--	--	--	--	--	--
	100	California	do	36	48	16	--	--	--	--	--	--	--	--	--	--	--	--
Botrytis byssoidea.	42	Wisconsin	do	--	2	--	26	56	14	2	--	--	--	--	--	--	--	--
	70	Illinois	do	--	--	6	24	28	32	10	--	--	--	--	--	--	--	--
	80	Wisconsin	do	--	4	6	34	36	18	2	--	--	--	--	--	--	--	--
	89	Illinois	Potato agar	--	--	6	28	32	26	8	--	--	--	--	--	--	--	--
			Onion	--	2	28	62	8	--	--	--	--	--	--	--	--	--	--
	90-1	do	Potato agar	--	--	--	68	30	2	--	--	--	--	--	--	--	--	--
	90-5	do	do	--	--	--	24	60	14	2	--	--	--	--	--	--	--	--
	90-7	do	do	--	--	6	38	26	12	4	4	--	--	--	--	--	--	--
	98	Wisconsin	Onion leaf	--	--	8	60	28	4	--	--	--	--	--	--	--	--	--
	101	do	do	--	24	28	48	--	--	--	--	--	--	--	--	--	--	--
	114	France	Onion	--	--	17	74	9	--	--	--	--	--	--	--	--	--	--
	94	Illinois	do	--	--	20	44	32	4	--	--	--	--	--	--	--	--	--
Botrytis squamosa.	27	Wisconsin	Potato agar	--	--	--	--	--	2	--	12	38	24	22	2	--	--	--
	30	do	do	--	--	--	--	--	--	2	--	4	22	36	24	10	2	--
	134	do	do	--	--	--	--	--	3	8	30	29	9	10	7	3	--	1

b Culture No. 65 was furnished by M. T. Munn, New York State Agricultural Experiment Station.

PATHOGENICITY

Munn (*20*) has already given conclusive proof of the pathogenicity of *Botrytis allii* upon onion bulbs. Many experiments have been performed by the writer in which the conidia or mycelium have been injected into wounds in the succulent scales. In general, when too rapid desiccation of the wounds was prevented and the bulbs were kept at any temperature between 5° and 20° C. positive infection resulted uniformly. The most satisfactory method of obtaining infection has been to inject conidia into needle wounds, placing bulbs in oiled paper bags and incubating them at 15° to 20°. Infection of bulbs by spraying spores on the unwounded surfaces of dry or succulent bulb scales was found by Munn (*20*) to be difficult to attain. The writer has likewise failed to produce infection by this means. It is evident, however, that the fungus may penetrate the unbroken cuticle of succulent scales. This was demonstrated by carefully inoculating the outer succulent scale of a bulb in the usual manner. After the resulting lesion had advanced to a certain point the outer scale was removed, and invasion of the adjacent underlying scale was found to have occurred. This experiment was repeated several times with uniform results. From this fact it is evident that when natural infection of a single scale takes place at the neck or through wounds at other points on the bulb the fungus is not necessarily confined to the scale originally infected. It is true that the fungus does spread more rapidly through the tissue of the first scale infected, but advance into adjoining scales is not precluded. However, initial infection through the unwounded outer scales apparently does not occur, or in any case is exceptional. When inoculation is made in the succulent tissue, the fungus decays the bulbs of colored and white varieties equally well. The nature of resistance of colored bulbs is discussed later in this paper.

When the onion plant is mature, infection may occur through the unwounded neck tissues, most of which by that time are dead or senescent. This has been shown by artificially inoculating bulbs with and without tops. For further discussion of these experiments the reader is referred to a subsequent section on "Relation of stage of maturity of host to infection of bulbs."

Munn (*20*) produced infection repeatedly by applying spores to the green leaves of plants in a humid atmosphere. Two experiments were performed by the writer in which spores were applied to leaves of vigorously growing plants which were then placed in a moist chamber at about 18° C. for 48 hours. Fine droplets of water covered the plants during this period, and conditions should have been ideal for infection. The plants were removed from the chamber to a greenhouse in which the temperature ranged from 15° to 20°. No infection became evident in either experiment. Several experiments were then performed in which the plants were left in the moist chamber for longer periods. After the first week the infection of some of the leaves was evidenced by the softening of the affected tissue, and this softening was followed by the characteristic sporulation of the organism on the decayed areas. Under these conditions, results quite similar to those of Munn were obtained. It seems to be necessary, however, to keep the plants in a very humid environment for fairly long periods in order to produce infection. When affected plants were removed to ordinary greenhouse environment, the progress of the fungus was almost, if not entirely, checked. The writer is inclined to consider the disease of the aerial parts other than the bulb caused by this fungus as a very mild type of parasitism, which takes place only under extreme and abnormal conditions. This evidence, together with field observations, would lead one to conclude that *Botrytis allii* is of strictly limited importance as a parasite of the aerial portions of the plant. Under extremely humid conditions it might cause slight damage, but how much of the action was truly parasitic and how much was mere subsistence upon senescent or dead tissue would remain an open question. Its occurrence on senescent or dead tissues is no doubt common, and its development upon dead leaves and dead tips of leaves during the growing season of the host is undoubtedly an important part of the life cycle of the oragnism. That the occurrence of Botrytis apparently damaged onion leaves has been reported in a few instances (*4, 5, 11, 17, 20*).

HOST RANGE

By artificial inoculation, bulbs of white multiplier onion (*Allium cepa* var. *bulbellifera*) and white shallot (*A. ascalonicum*) were found to be quite as susceptible to gray-mold neck rot as those of common onion. Garlic bulbs (*A. sativum*) were also readily infected, but the progress of the disease was much slower on these than on either of the hosts just mentioned.

MYCELIAL NECK ROT

SYMPTOMS

In the early stages of its development the mycelial neck rot is not readily distinguishable from the gray-mold neck rot. As in the latter, the usual avenue of infection is through the neck tissues, but occasionally cases are found where the invasion takes place by way of the stem plate or through wounds at other points upon the onion scales. The same water-soaked, sunken appearance typifies the newly infected tissue, and the advancing margins of the diseased area continue to show this symptom. The line of demarcation between healthy and diseased tissue is also usually well defined, and as in the case of *Botrytis allii,* the mycelial neck-rot organism initiates the breakdown of the host tissue somewhat in advance of the hyphae. In the older decayed parts the scales become shrunken, and grayish superficial mycelium develops in a manner not unlike that of *B. allii.* There is in the main, however, a greater quantity of superficial mycelium formed in the case of mycelial neck rot than would be the case with gray-mold neck rot under like environment. Recently inoculated bulbs of the two forms placed in moist chambers respond quite differently. In the case of gray-mold neck rot the organism sporulates promptly, with little additional superficial mycelium, while *B. byssoidea* usually produces a profuse quantity of mycelium, white at first but later turning gray with age. The most striking point of difference between the two forms is that the mycelial neck-rot organism sporulates very sparsely in these early stages, and it is often difficult to bring about conidial production on newly decaying bulbs even when the latter are placed in the moist chamber. As the mycelial neck rot progresses sclerotia commonly develop in the older decayed tissue. They resemble very closely those of *B. allii* in all respects. Sporulation occurs to some degree under sufficiently moist conditions on the older decayed tissue. The sporulating mass is light-gray at first, gradually becoming darker with age, the darker shade being due in the main to the wall coloration in the older portions of the conidiophores. As a rule the sporulating mass is distinguishable from that of *B. allii* because of the fact that the conidiophores of the latter are usually somewhat shorter, less branched, and more prolific, giving the appearance of a low dense mass of conidia. In the case of *B. byssoidea,* on the other hand, the conidiophores assume somewhat greater length, are more branched, and sporulate less profusely, giving in the end the appearance of a more fluffy development of aerial mycelium with a less dense conidial mass.

It will be seen from this description that points of macroscopic difference between the symptoms of the two diseases are not sufficiently marked to afford even the trained casual observer a ready means of distinction. The outstanding macroscopic distinguishing characters which one may use with reasonable accuracy after some experience in observing the two diseases are (1) the comparative lack of sporulation in mycelial neck rot and the abundance of sporulation in gray-mold neck rot, and (2) the fact that when sporulation does occur in mycelial neck rot, the ranker growth of conidiophores is usually noticeably different from the low dense growth of the sporulating hyphae of the gray-mold neck rot. Distinction is made the more difficult by the fact that at times the two forms may be found together upon the same bulb. Very often one who is work ng constantly with the two diseases finds it necessary to resort to artificial culturing of the organisms to make diagnosis certain. Growing the organisms upon potato-dextrose agar is a ready means of distinguishing between them. (See fig. 5.) *Botrytis allii* will invariably sporulate abundantly with a few days, while the mycelial neck-rot organism produces rank-growing, fluffy, white aerial mycelium, with seldom, if ever, any evidence of sporulation. Certain aspects of the disease are shown in Figures 2 and 3.

THE CAUSAL ORGANISM (BOTRYTIS BYSSOIDEA)

The mycelium of *Botrytis byssoidea* has no characters by which it may be readily distinguished from *B. allii.* The appressoria or holdfasts are also very similar in the two species. Sclerotia are formed in the same manner and are much alike as to size, shape, and color.

The conidiophores of *Botrytis byssoidea,* like those of *B. allii,* originate either from the free mycelium or from the sclerotia, and their development and the method of spore production in the two forms is of the same general type. A few points of difference in detail are to be noted. Conidiophores are produced much less commonly on the decayed host tissue in *B. byssoidea,* and they are seldom found on artificial media. When produced upon decaying onion scales they are noticeably more scattered than the conidiophores of *B. allii;* permanent branches are formed a little more commonly; and the production of spores is not so profuse. The conidiophores are hyaline at the growing tip, and the walls turn brown promptly as they grow older. To the naked eye the fungus as it fruits upon onion tissue presents a less crowded, more cottony, and somewhat more elevated appearance than the low dense gray-mold development of *B. allii.* The fertile tips of the conidiophores branch and produce spores in the same manner as described in connection with *B. allii.* (Fig. 6, M.) The sporiferous side branches usually degenerate as far back as the septum, which is laid down close to the main trunk of the conidiophore (fig. 6, N); occasionally one persists and continues to grow out as a permanent fertile branch. In this form, as in *B. allii,* the branches, whether permanent or not, show a marked constriction at the point of juncture with the main trunk when they have reached their maximum diameter, and in the case of the permanent branch this constriction remains. As in the other forms, it is common for the conidia to adhere to the sides of the main trunk of the conidiophore until they are removed by water or air currents. The scars left by the degenerated fertile branches are quite similar to those of *B. allii.*

The conidia of *Botrytis byssoidea* are very similar to those of *B. allii* in shape, color, and mode of germination. (Fig. 6, O.) They are occasionally a little longer in relation to their width and thus have a more oblong appearance. They vary considerably in size (8 to 20 by 5 to 11 μ), but, as is shown in Table 1 the majority fall within the limits of 10 to 16 by 6 to 8 μ. They therefore will constantly average somewhat larger than those of *B. allii,* both upon onion tissue and when they are occasionally produced upon potato agar. Microconidia, globose and about 3 μ in diameter, are occasionally formed.

FIG. 2.—Comparison of gray-mold and mycelial neck rots. Healthy White Portugal onion sets inoculated after harvest by the injection of spores or mycelium through neck wounds, placed in standard storage crates, and left in an onion-set warehouse at Morton Grove, Ill., for eight weeks. Those in the upper row were inoculated with *Botrytis allii*. Note the characteristic gray mold on the decayed tissue. The lower five bulbs were inoculated with *B. byssoidea*. Note the absence of conidia and the development of aerial mycelium and of sclerotia on the decayed tissue

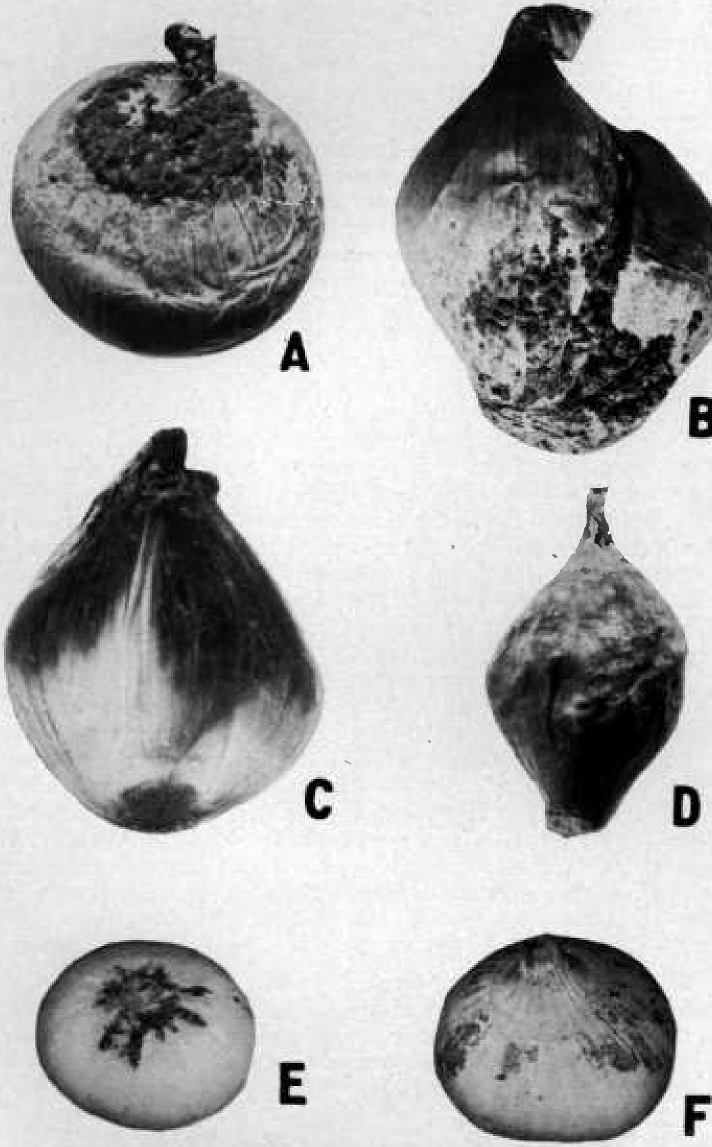

FIG. 3.—Mycelial neck rot *Botrytis byssoidea* on White Globe (A to D) and White Portugal (E, F) onions. Note the formation of sclerotia on the older decayed tissue (A, B). Basal infection commonly occurs (B). The first evidence of infection of the tissue is a water-soaked appearance; the decayed tissue becomes permeated with mycelium and gradually shrivels (C). An abundance of superficial mycelium is common (D). An early stage of infection at the neck is shown in F. Occasionally rapid desiccation of newly infected scales checks the further progress of the fungus (F)

PATHOGENICITY

The mycelial neck-rot disease has been produced repeatedly by inoculating onion bulbs through needle wounds with mycelium from pure culture and with conidia and conidiophores which developed upon naturally infected or upon artificially inoculated bulbs. As in the case of *Botrytis allii*, the most uniform results were obtained when too-rapid desiccation of the wound tissue was prevented. The most satisfactory results were obtained by placing the inoculated bulbs in oiled paper bags and incubating them at 15° to 20° C. Under these conditions the characteristic bulb rot occurred, and the progress of the decay was approximately equal to that of gray-mold neck rot. Under humid conditions and favorable temperature, invasion of the unwounded outer succulent scales has been noted, and the spread from scale to scale through the unbroken cuticle has been demonstrated. Initial infection through the dry outer scales or through the unbroken outer succulent scale does not commonly occur in nature, however, and there is little evidence of natural invasion except by way of wounds or the dying tissues at the neck of the bulbs.

With respect to leaf infection, what has already been said of a gray-mold neck rot may well apply to mycelial neck rot. No evidence has been found in nature that this organism causes a serious blight of onion tops. It is commonly found fruiting upon dead or senescent leaf tissue during humid weather, but is to be regarded as little more than a saprophyte. Vigorously growing onion plants inoculated with a spore suspension of the organism and kept in a moist chamber at about 18° C. for 48 hours and removed to a greenhouse at 15° to 20° did not yield evidence of infection. As in the case of *Botrytis allii*, plants inoculated in such a manner and kept under very humid conditions at 15° to 20° for one to two weeks eventually showed evidence of leaf infection. It is questionable, however, if this situation commonly exists naturally in onion-growing regions in the United States. *B. byssoidea* was found in one instance causing secondary infection of seed stems of Egyptian onion that has been infected with rust (*Puccinia asparagi*) (*30*). In the original report this was not considered to be a neck-rot form, since first inoculations of the bulbs gave negative results. When the proper conditions for infection were later determined, positive infection of bulbs with this strain was obtained.

HOST RANGE

Bulbs of white multiplier onion and of white shallot when inoculated with *Botrytis byssoidea* decayed quite as rapidly as did those of common onion. Bulbs of garlic were also successfully inoculated, but, as in the case of *B. allii*, the progress of the disease was distinctly slower than upon the other hosts.

SMALL SCLEROTIAL NECK ROT

SYMPTOMS

The small sclerotial neck rot has so far, with one exception, been found only upon white varieties of onion. In one instance it was found in a few very slightly pigmented bulbs which appeared in a lot of Yellow Globe variety and were probably the result of previous crossing with a white variety. As will be pointed out later, colored bulbs are readily infected when inoculated through wounds in the succulent scales. The fungus most commonly appears first near the neck of the bulb and, as a rule, not until some weeks after the crop has been harvested and stored. It is often confined to the two or three dry outer scales. At times it is found upon the succulent scales, commonly in association with the mycelial neck rot.

Usually the first evidence of the disease is the appearance of very thin, scalelike sclerotia which adhere very closely to the dry scales. The sclerotia are at first light colored, but most of them turn completely black with age. In many instances their development is arrested prematurely, and bodies which are light gray in the center and black only at the margin result. The sclerotia are usually roughly circular and measure from ½ to 1½ mm. in diameter. They vary from this form, however, being sometimes larger and more irregular in shape. The mycelium of the fungus is scanty and not often distinguishable microscopically upon the affected dry outer scales. When it does appear it is scattered and has a dark-green cast. Sporulation occurs on conidiophores, arising most commonly from the sclerotia and more rarely from the scattered mycelium. At room temperature very little sporulation can be induced even when affected scales are placed in a moist chamber, but under moist conditions in the ice box or at temperatures between 5° and 18° C. sporulation upon the sclerotia is common.

The decay of the succulent scales is distinctly slower than that caused by either *Botrytis allii* or *B. byssoidea.* The cytolytic action in advance of the hyphae, characteristic of the other two forms, prevails in this case as well. The newly rotted area is water-soaked in appearance, and there is a quite definite margin between diseased and healthy tissue. In the older decayed portions grayish superficial mycelium is formed, though usually rather scantily, while sclerotia are also commonly embedded in the rotted tissue. The decayed portions of the bulb often become distinctly brownish in color, and in this respect the disease is distinct from the gray-mold and the mycelial neck rots. Certain aspects of the disease are illustrated in Figure 4.

THE CAUSAL ORGANISM (BOTRYTIS SQUAMOSA)

The mycelium of the small sclerotial form is not sufficiently different from that of the other two onion Botrytis forms to be of diagnostic value. Appressoria are commonly produced. The sclerotia are quite characteristic. They vary in size from ½ to 1½ mm. or more, and often converge into large, irregular scalelike crusts. On the host they are almost always very thin and flat and seldom acquire the thickness of ½ mm. They are usually roughly circular, but occasionally they are quite irregular in form. They appear first as dense, thin mycelial mats of a dirty-white color. They become darker with age and gradually become black, the color appearing first at the outer margins and progressing inwardly until the whole sclerotium is deep black. Occasionally the development of color is arrested prematurely, with the result that the sclerotia have light grayish centers and black margins.

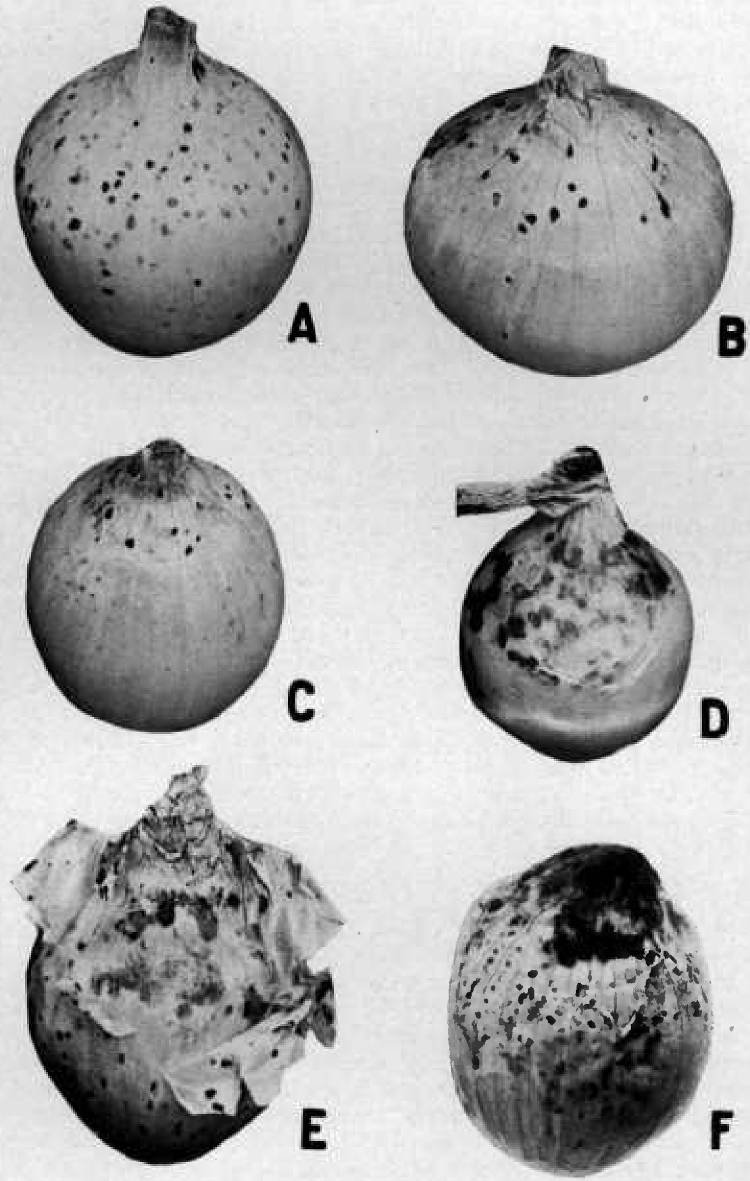

FIG. 4.—Small sclerotial neck rot *Botrytis squamosa* on White Globe onions. Thin, flat, black sclerotia develop commonly on the dry outer scales. Invasion of the succulent scales sometimes occurs (D, E). In F, *Botrytis byssoidea* is also present in the succulent scales. The larger, more rounded sclerotia near the neck of the bulb are those of the latter fungus

The conidiophores arise occasionally directly from free mycelium, but in the main are produced upon the sclerotia. They are hyaline at the growing tip, but the walls turn dark promptly as they become a little older. They are septate, and occasionally branched, the branches being constricted at the point of juncture with the main stalk. Previous to sporulation the growing tip gives rise to a number of branches which rebranch and at their rounded tips send out sterigmata upon which the conidia are borne in the same manner as described for *B. allii* and *B. byssoidea.* (Fig. 6, J.) The sporulating branches are, as a rule, shorter and plumper than those described for the other two forms. As the spores mature, the branches, having been cut off close to the main stalk by septa, rapidly degenerate. As they do so the walls of these branches contract in a unique manner and give the appearance of closing together in folds suggestive of the contracting bellows of a camera. (Fig. 6, K.) The spores, if not removed by air current or by water, adhere in a group to the sides of the main stem of the conidiophore which now proliferates by growing upward, again branching and sporulating. Scars or knobs not unlike those previously described for the other two species mark the points at which degenerating sporiferous branches are attached. Occasionally one of the branches becomes permanent.

The conidia are hyaline, ovoid, and continuous, and germinate within 24 hours under favorable conditions by each sending out usually one hyaline germ tube. (Fig. 6, L.) Septation of the spores upon germination is not common. They vary in size from 13 to 24 μ by 9 to 18 μ, but the majority of them fall within the limits of 15 to 22 by 11 to 15 μ. (See Table 1.) Microconidia, globose and about 3 μ in diameter, are occasionally formed.

PATHOGENICITY

Inoculation of healthy onion bulbs was brought about by injecting mycelium or sclerotia from pure cultures of *Botrytis squamosa* into needle wounds made near the necks. The bulbs were placed in oiled paper bags and incubated at various temperatures. The most rapid decay occurred at about 16° C., although infection did occur over a range of 4° to 22°. Even at the optimum the decay progressed much more slowly than in the case of *B. allii* or *B. byssoidea.* Results were obtained, however, which left no doubt that the organism is pathogenic upon the succulent scales and that under these conditions colored bulbs decayed quite as readily as white bulbs. Direct infection through the unwounded surface of the succulent scale occurs under proper conditions of humidity and temperature, although this does not appear to be the usual method of initial infection.

Vigorously growing onion plants were inoculated with a spore suspension of the organism and transferred at once to a saturated atmosphere held at about 18° C. After 48 hours the plants were transferred to a greenhouse kept at 15° to 20°. No evidence of infection developed. When plants were left in the moist chamber for a week or more, leaves were attacked in the manner already described in connection with *Botrytis allii* and *B. byssoidea. B. squamosa* was somewhat more aggressive under these conditions than were the other two species. Severely infected plants, when removed to ordinary greenhouse conditions, rapidly outgrew the disease. It appears, therefore, that in an extremely humid environment having a favorable temperature, infection of the aerial parts by *B. squamosa* may occur. But, as in the case of the other two neck-rot organisms, there is little evidence that this form causes a destructive leaf blight, and its relation to the host during the growing season is primarily one of subsistence on dead or senescent tissue.

Infection of bulbs through the unwounded neck has not been produced by artificial inoculation, but the common observation of the disease upon bulbs regardless of whether the tops were clipped at harvest shows that the organism penetrates the scales by way of the senescent leaf tissue without the aid of artificial wounds.

COMPARATIVE STUDIES OF THE THREE NECK-ROT ORGANISMS

CULTURAL CHARACTERS

All three species of Botrytis associated with onion neck rot grow readily upon onion and potato-dextrose agar. On either of these media the growth characters of each species are quite distinctive, and they afford a convenient means of differentiation. It has not been found necessary to study the development of these fungi on a wide range of artificial media. Potato agar containing 2 per cent dextrose has been used as stock medium, and the salient characters of growth on this agar will be given.

BOTRYTIS ALLII (fig. 5, A)

On potato-agar plates a rapidly growing colony was produced, which attained a diameter of about 50 cm. in 4 days at 20° to 22° C. In the beginning the center of the colony consisted of dense whitish aerial mycelium, while the outer zone, about 5 mm. in width, consisted of scanty, creeping, extending mycelial threads. Conidiophores and conidia appeared on about the third day, nearly white at first, turning smoky gray with age. Eventually the entire plate became covered with a dense uniform layer of conidiophores. Sclerotia were not usually produced but occasionally developed in test-tube cultures with this medium. Dark-colored appressoria were sometimes formed when the mycelium penetrated the agar layer and came in contact with the glass plate, but here again the development was more pronounced in test-tube cultures at the edge of the slant. There was little difference in growth to be noted when maltose, lactose, or galactose was substituted for dextrose in the medium. Onion-scale agar and potato agar made without the addition of sugar produced growth quite similar to that on potato-dextrose agar, the chief point of difference being the smaller amount of appressorial development. The organism was carried for seven years on potato-dextrose agar without any noticeable change in growth characters, and this period of artificial culturing did not change the pathogenicity of the fungus.

BOTRYTIS BYSSOIDEA (fig. 5, B)

On potato-dextrose agar plates the *Botrytis byssoidea* colony grew somewhat faster at 20° to 22° C. than did *B. allii*. Abundant white, fluffy, aerial mycelium was formed, which was more raised and cottony than that of either *B. allii* or *B. squamosa*. It was fairly uniform in density except at the narrow outer zone of extending

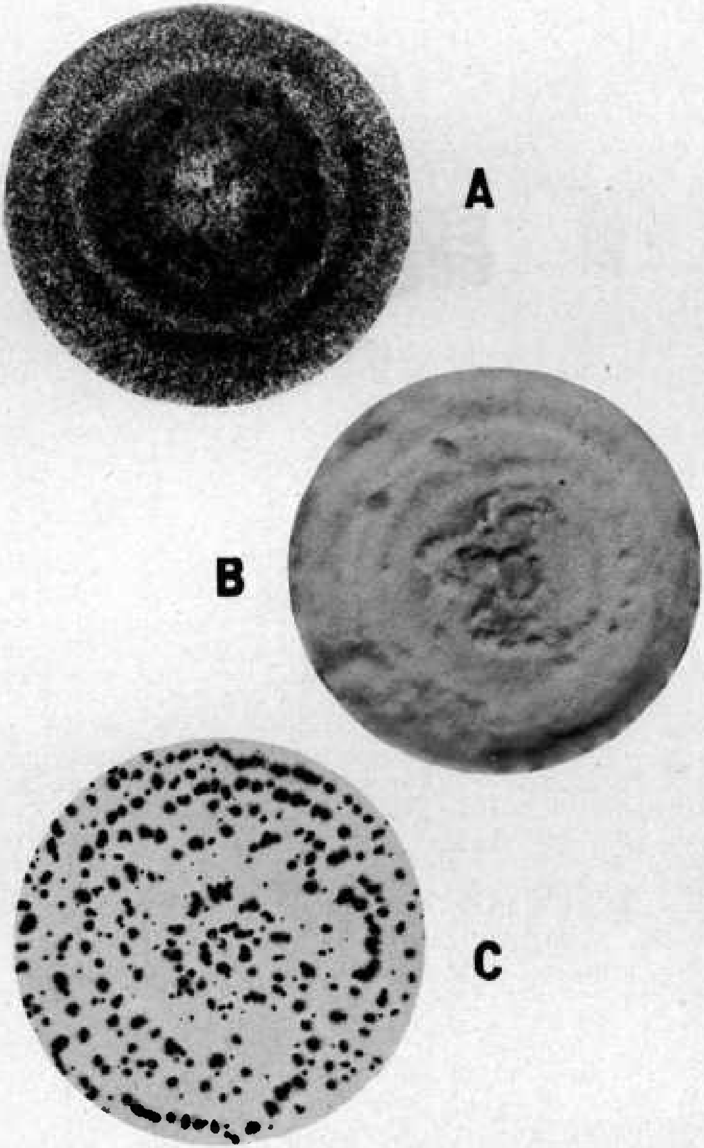

FIG. 5.—The three onion neck-rot organisms on potato-dextrose agar. A, *Botrytis allii*. Profuse production of conidia. B, *Botrytis byssoidea*. Profuse mycelial development but no conidia. C, *Botrytis squamosa*. Mycelial development followed by production of sclerotia. No sporulation occurred at room temperature, 20° to 22° C. After two months the culture was removed to the ice box, where profuse sporulation took place. Note the conidiophores arising from the sclerotia

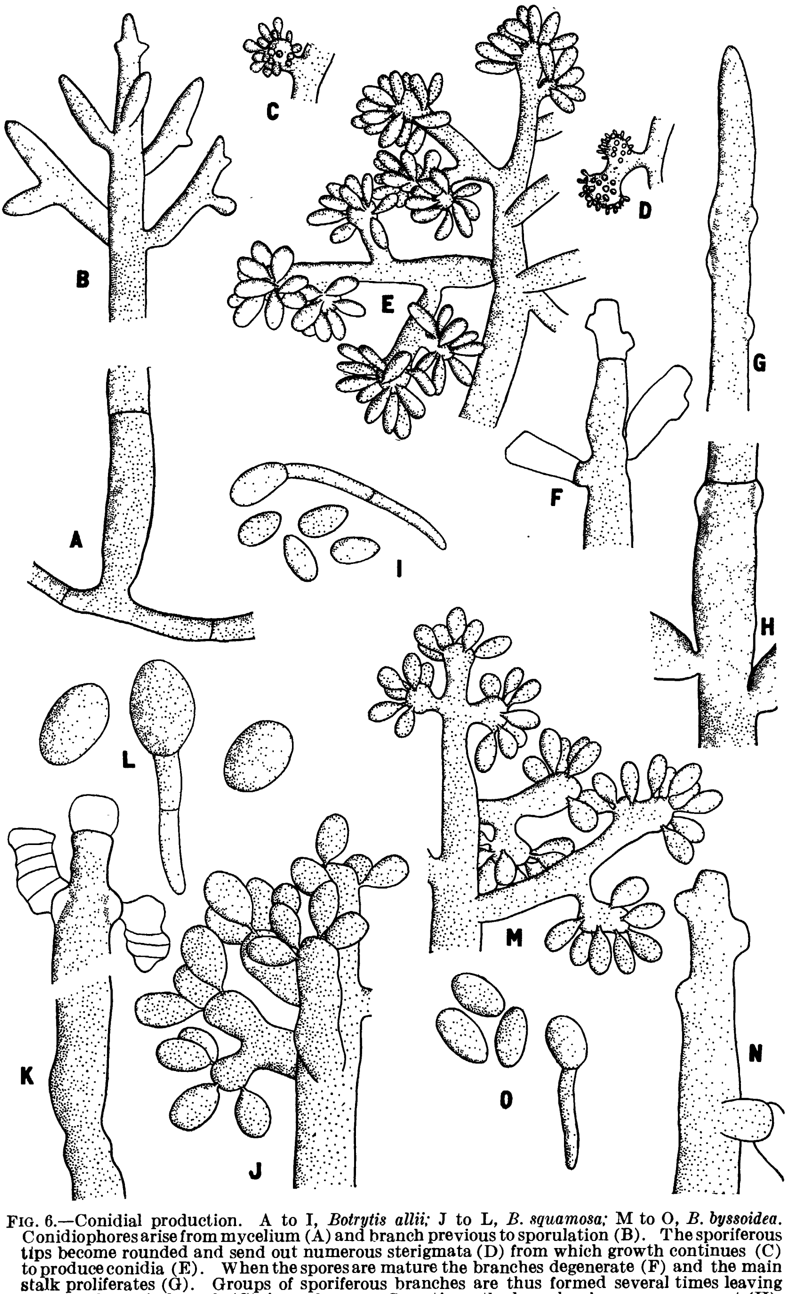

FIG. 6.—Conidial production. A to I, *Botrytis allii;* J to L, *B. squamosa;* M to O, *B. byssoidea.* Conidiophores arise from mycelium (A) and branch previous to sporulation (B). The sporiferous tips become rounded and send out numerous sterigmata (D) from which growth continues (C) to produce conidia (E). When the spores are mature the branches degenerate (F) and the main stalk proliferates (G). Groups of sporiferous branches are thus formed several times leaving scars on the main branch (G) in each case. Sometimes the branches become permanent (H). The process is similar in each species (J, K, and M, N). Note characteristic accordionlike folds in degenerating sporiferous branches of *B. squamosa* (K). See further explanation in text

hyphae. Conidia were seldom produced. Appressorial development was pronounced at the edge of test-tube slant cultures. Sclerotia were usually absent in both plate and tube cultures grown at room temperatures. In young tube cultures placed out of doors on January 25, 1926, at Madison, Wis., numerous characteristic sclerotia had formed when they were brought in on March 19. In another culture, about a month old when placed out of doors on December 5, 1925, and brought in on March 19, 1926, sclerotial formation did not take place but conidial production was quite pronounced. When maltose, lactose, or galactose was substituted for dextrose no conspicuous change in growth characters resulted. On onion agar and potato agar without dextrose the mycelial production was somewhat less profuse. Whereas *B. allii* was carried on potato-dextrose agar indefinitely without loss of pathogenicity, *B. byssoidea* usually lost entirely its pathogenicity within a few months under such treatment, especially when kept at room temperatures (20° to 22°). This change was accompanied by a reduction in the vigor of the culture as exhibited by less profuse aerial mycelium and less appressorial development.

Botrytis squamosa (fig. 5, C)

On potato-agar plates the *Botrytis squamosa* colony enlarged more slowly than either *B. allii* or *B. byssoidea*. It consisted of white, fluffy, aerial mycelium, except for the outer advancing zone, but was less raised and fluffy than *B. byssoidea*. Numerous sclerotia appeared over the entire plate after two to three weeks, first as dense whitish mycelial masses which became hard and black with age. They were mostly 1 to 2 mm. in width and thicker and more rounded on the upper surface than those which developed upon the host. There was very little sporulation at room temperature (20° to 22° C.), but profuse production of conidiophores arising directly from the sclerotia occurred at 12° to 16°. Substituting maltose and lactose for dextrose made little difference in the growth produced. When galactose was used, however, the sclerotia assumed a distinctly different form. They were a little larger, more irregular in shape, very thin and flat, and embedded just at or slightly below the surface of the substrate. On onion agar and potato agar made up without the addition of sugar fewer sclerotia were produced.

OVERWINTERING AND SEASONAL CYCLES

Experiments were undertaken to determine by what means the three neck-rot organisms might live through the winter at Madison, Wis. Sclerotia and spores on bulbs affected by mycelial and gray-mold neck rot were exposed to prevailing weather from December to March in the winter of 1925–26 by placing them in wire baskets on an outer window sill. Both sclerotia and spores of each organism were viable at the end of this period. Pure cultures were exposed over the same period, and they also remained viable. A culture of the small sclerotial neck-rot organism containing sclerotia and conidia was also exposed. Transfers from sclerotia as well as from the conidia and conidiophores were made at the end of the period with positive results in each case. It is thus apparent that the sclerotia will withstand winter weather, while it is not improbable that the mycelium and spores under certain conditions may also live through the extremely cold portion of the year.

From general field observations it is quite evident that each of the organisms persists from year to year in the soil or on refuse. The organisms from such materials are undoubtedly the beginning of saprogenic development the following season, when they live as saprophytes upon dying onion leaves and other organic matter during the growing season of the host. Spores from this saprogenic phase of the organisms are the source of inocula for bulb infection at and after the end of the growing season.

TEMPERATURE RELATIONS

Growth on Media

The relation of temperature to the range and rate of growth of the three organisms was studied upon potato-dextrose agar. Separate slants were inoculated each with one of the three organisms and placed in constant-temperature incubators the temperature of which ranged from 3° to 33° C. The three organisms responded quite similarly to the various temperatures. Growth ensued very slowly at 3° to 4°. There was a gradual increase in the rate of growth with increase in temperature up to about 20° while the rate was about the same between 20° and 25°. At 28° there was decidedly less growth than at the optimum, and at 30° there was still greater retardation. At 33° there was some growth of each organism, but it was very meager in all cases. Thus all three forms grew upon potato-dextrose agar within the range of 3° to 33°, the growth being very slow at either end of the range and most rapid at about 20° to 25 °.

Spore Germination

Germination tests were conducted at various temperatures with the conidia of each of the three species. Spore suspensions were made in tap water and drops transferred to clean glass slides, which were placed in moist chambers in the incubators. In Table 2 the rate of germination in each incubator is given. Spores of *Botrytis squamosa* germinated more promptly than those of the other two species. It is to be seen that germination occurred more promptly at temperatures between 19° and 27° C. than at temperatures below 19°, but, on the other hand, it took place over the entire range of temperature with each species after a period of 24 hours.

Table 2.—*Relation of temperature to spore germination* [a] *of Botrytis allii, B. byssoidea, and B. squamosa*

Temperature °C.	Species and interval											
	Botrytis allii				Botrytis byssoidea				Botrytis squamosa			
	4 hours	8 hours	12 hours	24 hours	4 hours	8 hours	12 hours	24 hours	4 hours	8 hours	12 hours	24 hours
3.5–4	0	0	0	+	0	0	0	+	0	0	0	+
6.5–7	0	0	0	+	0	0	0	+	0	0	0	+
8.5–10	0	0	0	+	0	0	0	+	0	0	0	+
13.5–15	0	0	+	+	0	0	+	+	+	+	+	+
16.5–18	0	0	+	+	0	0	+	+	+	+	+	+
19.5–20	0	+	+	+	0	+	+	+	+	+	+	+
22.5–23	0	+	+	+	0	+	+	+	+	+	+	+
24.5–25.5	0	+	+	+	0	+	+	+	+	+	+	+
26.5–27	0	+	+	+	0	+	+	+	0	+	+	+

[a] + indicates germination; 0 indicates no germination.

Sporulation

It is of course important to know the bearing of temperature upon the production of spores of the fungi when exposed to properly humid conditions. *Botrytis allii* appears to sporulate readily at comparatively low relative humidity, but that the other two forms do is not so evident. *B. allii* sporulates readily in culture or upon rotted onion tissue over a range of 4° to 25° C. *B. byssoidea*, although it does not sporulate readily in culture, will do so when old decayed onion tissue is placed in a moist chamber. Under these conditions *B. byssoidea* produces conidia most quickly at about 23° but quite promptly within a range of 13° to 27°. At temperatures between 3° and 13° it sporulates more slowly. *B. squamosa* has a more limited range of sporulation. No conidia have been found at 22° either in pure cultures or on decayed tissue kept in a moist chamber. The range at which sporulation ordinarily occurs under these conditions is about 18° to 3°. The optimum is about 16°.

Infection and Progress of Decay

A number of experiments were made to determine the relation of temperature to infection and the rate of progress of decay. The bulbs were all inoculated by injecting mycelium or spores into needle wounds near the neck. They were then placed either in oiled paper bags or in uncovered paper boxes and incubated at different temperatures. The first two experiments are concerned with *Botrytis allii* and *B. byssoidea*. In the first experiment, the results of which are given in Table 3, the bulbs were all placed in oiled paper bags.

Table 3.—*The relation of temperature to infection and progress of decay of onion bulbs inoculated with Botrytis allii and B. byssoidea; five bulbs in each lot; Red Wethersfield variety*

Temperature °C.	Botrytis allii		Botrytis byssoidea		Control
	Per cent infected	Rate of progress[a]	Per cent infected	Rate of progress[a]	Per cent infected
2–4	80	1	100	1	0
5–8	100	2	100	2	0
10–11	100	3	100	3	0
15.5–16.5	100	4	100	4	0
18.5–19.5	100	4	100	4	0
23–23.5	100	3	100	3	0
26.5–27.5	0	----------	20	1	0
28.5–29.5	20	1	20	1	0
32–34	0	----------	0	----------	0

[a] 1 indicates the least rapid and 4 the most rapid decay.

The temperatures below 20° C. were maintained in an incubator where the humidity was quite high; but in the incubators at higher temperatures the humidity was correspondingly lower, and the oiled paper bags did not entirely prevent the desiccation of the decaying bulbs. Thus the possible influence of humidity as a limiting factor must be considered. It is to be seen that in this experiment the most rapid decay occurred at 15° to 20°, while above 26° the amount of infection and the rate of decay were decidedly limited.

Another series of experiments was run to determine whether infection would be accelerated at the higher temperatures if a high relative humidity prevailed. Two chambers in which the temperature was 25° to 27° and 28° to 30°, respectively, were kept at saturation. Inoculated bulbs were placed in open boxes in each. At the same time boxes of inoculated bulbs were placed in other chambers having different temperatures and different relative humidities. In the latter series the environment was not controlled as accurately as was desired, but the average temperatures and relative humidities as recorded on thermographs and hygrographs are given, and the results are included for their comparative value. (Table 4).

TABLE 4.—*The relation of temperature and humidity to decay of onion bulbs by Botrytis allii and B. byssoidea; 10 bulbs in each lot; Red Wethersfield variety*

Temperature °C.	Relative humidity per cent	Botrytis allii, per cent infected	Botrytis byssoidea, per cent infected	Control, per cent infected
10°±	60±	100	100	[a] 10
15°±	50–75	100	100	0
15°–20°	75–85	100	100	0
22°–25°	60–80	100	100	0
22°–27°	60–75	70	80	0
25°–30°	75–85	70	20	0
25°–27°	100	100	100	0
28°–30°	100	0	0	0

[a] One of 10 bulbs became infected by *Botrytis allii* during the experiment.

At temperatures below 20° C. the results were similar to those in the previous experiment. At temperatures above 20° the relative humidity was higher than in the previous experiment. Here it is evident that the higher humidity accelerated infection, although as was noted before, the progress of decay was distinctly retarded as the temperature rose above 22°. A comparison of the lots held at 100 per cent relative humidity at 25° to 27° and 28° to 30° shows that the maximum temperature for infection is somewhere between 27° and 30°. It is also significant that throughout these experiments *Botrytis allii* and *B. byssoidea* reacted very similarly to temperature. In Figure 1 are shown the relative amounts of decay in bulbs inoculated with *B. allii* and *B. byssoidea*, respectively, and held in moist chambers at 18°, 23°, and 26°.

Two experiments of a similar nature were run with *Botrytis squamosa*. The bulbs were placed in oiled paper bags in an incubator at temperatures ranging from 23° to 4° C. Infection occurred over the entire range. The most rapid decay took place at about 15°. At 18° it was nearly as rapid as at 15°. At 23° it was distinctly retarded, but desiccation was somewhat greater than at the lower temperatures. Below 15° there was a gradual slowing up of activity roughly proportionate to the reduction in temperature.

RECAPITULATION

The data which have just been noted point to the conclusion that all three fungi are favored by temperatures between 15° and 20° C. It is true that mycelial development is somewhat more rapid and conidial germination a little prompter between 20° and 25°, but on the other hand the infection studies show quite clearly that the diseases progress less rapidly above 20° than between 15° and 20°. Sporulation in *Botrytis allii* and *B. byssoidea* occurs over a wide range if the atmosphere is humid, and this holds true even in the saprophytic stage of the fungi during the growing season of the host. *B. squamosa* is more limited in this respect, inasmuch as there appears to be little or no sporulation above 20°.

It may thus be assumed that humid cool weather during the growing season of the onion plant is most favorable to the development and spread of the neck-rot fungi, while hot dry weather is correspondingly less favorable. The small sclerotial neck-rot organism is probably the one most retarded by higher temperatures, and this belief is supported by the fact that it is usually not found in midwestern districts until some weeks after the appearance of mycelial neck rot. At harvest time, when infection of the bulbs commonly occurs, warm dry weather is least favorable to infection, and in fact incipient infection of mycelial neck rot has often been found to be completely checked by such an environment.

As substantiating these views some evidence from field observations on the occurrence of mycelial neck rot over a period of years in southeastern Wisconsin may be cited. In this district two severe epiphytotics have occurred in the decade from 1915 to 1924. In 1915 the disease was very severe even in the resistant Red Globe variety, while in 1924 the damage to this variety was nearly as great, and with the white varieties it approached a complete loss. In contrast with these two years, the season of 1919 was one of great scarcity of neck rot. Climatically, 1915 and 1924 represent one extreme and 1919 the other. An examination of the weather records taken by the United States Weather Bureau at Racine, Wis., give some tangible details. The season of 1915 was one of abundant rainfall, the total precipitation from June 1 to September 30, inclusive, being 15.76 inches, which was 2.92 inches above normal. The mean temperatures for June, July, and August were, respectively, 3.8°, 4.3°, and 4.4° F. below normal, while that for September was 1.4° above normal. In the season of 1924 the precipitation was 6.76 inches above normal, while the mean temperatures of the four months were, respectively, 2.2°, 0.7°, 1.3°, and 4.3° below normal. In 1919 the precipitation for the four-month period was only 0.17 inch above normal, while the mean temperatures were 5.9°, 4.9°, 1.4°, and 3.2° above normal. During the 1915 and 1924 periods there were, respectively, 77 and 49 days of cloudy or partly cloudy weather, while in 1919 there were only 37 such days. Thus the two epiphytotic years were unusually moist, cool, and cloudy during the major portion of the onion-growing season; while the year of least disease of the decade was unusually dry, warm, and clear during the corresponding period.

It is to be expected, from what we know of the life history of the Botrytis forms, that moist, cool, cloudy weather is most favorable to the saprophytic development of the organism during the growing season of the onion. The same conditions are noticeably effective in delaying the maturity of the crop and tend to develop plants which are more succulent at the neck and thus slower to desiccate at the point where Botrytis infection occurs. Furthermore, such weather is most conducive to infection at the critical time. This fact was most noticeable in 1915 when maturity was delayed some three weeks, and the frequent rains during the harvest period made proper curing almost impossible. In 1924 the delay of harvest was not so great, but careful examination showed the organism to be widespread and fruiting abundantly on old leaves and the dying tips of the leaves just previous to pulling of the crop. The clear, hot, drying weather of 1919, on the other hand, was unfavorable to the multiplication and spread of Botrytis during the season, a fact which tended to reduce the amount of natural inoculum at harvest time. Moreover, the maturity of the host plant was hastened under such conditions, and the top growth was so reduced as to facilitate rapid and thorough desiccation of the neck. It seems quite likely that the influence of climatic conditions is exerted in three important directions: First, they create conditions favorable or unfavorable to the multiplication of the parasite; second, they prolong or shorten the period of growth of the host and influence the degree of succulency of the neck at harvest time; third, they influence infection at the critical time by either favoring or retarding the germination and growth of the causal organism.

RELATION OF STAGE OF MATURITY OF HOST TO INFECTION OF BULBS

It has already been intimated that the condition of the host tissues at the time of exposure to the parasites is important in determining infection. Some laboratory experiments will be reported which were designed to study this point.

LABORATORY EXPERIMENTS WITH BOTRYTIS ALLII

Experiment 1

Three varieties of onion, White Portugal, Yellow Globe, and Red Globe, were grown on soil which had not produced this crop for at least five years. When the tops of the plants had fully matured the bulbs were pulled. Two groups from this lot of bulbs were prepared. In one group tops were left intact; in the other they were clipped sufficiently near the bulb to expose the succulent tissues of the scales. The two groups were again divided into equal parts, one part in each case being used as a control, the other for inoculation. The controls were sprayed with sterile water, while the remaining bulbs were sprayed with a conidial suspension of *Botrytis allii*. The controls and the inoculated bulbs were then placed in separate wire baskets and kept in a room having a fairly constant temperature of about 18° C., where they were suspended in a partially closed chamber over moistened sphagnum moss. The inoculations were made on September 3, and the bulbs were examined on September 22. The final data are noted in Table 5.

TABLE 5.—*Development of Botrytis allii in topped and untopped bulbs of three varieties of onion; experiment 1*

Variety	Method of handling tops	Inoculated		Control	
		Total number of bulbs	Number with neck rot	Total number of bulbs	Number with neck rot
White Portugal	Topped	20	17	20	0
Do	Untopped	20	0	20	0
Yellow Globe	Topped	10	8	10	0
Do	Untopped	10	1	10	0
Red Globe	Topped	10	5	10	0
Do	Untopped	10	0	10	0

The outstanding result is that whereas infection took place quite readily when the succulent tissue was exposed, only 1 bulb out of the 40 which were exposed to the inoculum with the tops intact became diseased.

EXPERIMENT 2

The experiment reported above was repeated with some modifications. Red, Yellow, and White Globe plants were pulled, and the tops were allowed to cure out thoroughly. They were then divided into four groups and prepared for inoculation in the following ways: (1) The tops were cured down but not removed; (2) 1 to 2 inches of thoroughly cured neck were left intact; (3) no neck tissue was left, but since the tops were thoroughly cured down to the bulb proper no succulent tissue was exposed; (4) the necks were so removed as to expose wounded, succulent tissue. A portion of each lot was then sprayed with a conidial suspension of *Botrytis allii;* a second portion was sprayed with conidial suspension and covered with moistened filter paper; a third portion was sprayed with sterile water and covered with moistened filter paper to serve as a control. All three lots were stored in shallow trays at about 18° C. The inoculations were made on September 23. The final observations, made on November 27, are recorded in Table 6.

TABLE 6.—*Relation of neck tissue to infection of Botrytis allii in bulbs of White, Yellow, and Red Globe varieties; experiment 2*

Condition of neck tissue	Variety	Inoculated and not covered		Inoculated and covered with moistened filter paper		Sprayed with sterile water and covered with moistened filter paper	
		Number of bulbs	Number with neck rot	Number of bulbs	Number with neck rot	Number of bulbs	Number with neck rot
Untopped	White	25	0	27	1	26	0
	Yellow	25	0	27	0	25	0
	Red	25	0	26	0	25	0
1 to 2 inches of the neck left intact	White	25	0	25	0	25	0
	Yellow	49	0	27	0	3	0
	Red	29	0	26	0	28	0
No neck tissue left; succulent tissue not exposed	White	25	0	25	0	17	0
	Yellow	25	0	25	0	27	0
	Red	25	0	27	0	24	0
Tops clipped so as to expose wounded tissue	White	25	9	23	11	25	0
	Yellow	25	6	29	15	25	0
	Red	25	1	30	13	25	0

It is again evident that the desiccated neck tissue is, under the conditions of the experiment, an effective barrier against the invasion of *Botrytis allii*.

LABORATORY EXPERIMENT WITH BOTRYTIS BYSSOIDEA

EXPERIMENT 3

With bulbs from the same lot used in experiment 1 a comparable experiment was conducted at the same time, wherein inoculations were made by spraying with a conidial suspension of *Botrytis byssoidea*. Inoculation was made on September 3 and the final data were recorded on September 22. (Table 7.)

TABLE 7.—*Development of Botrytis byssoidea in topped and untopped bulbs of three varieties of onion; experiment 3*

Variety	Condition of tops	Inoculated bulbs		Control bulbs	
		Total number	Number with neck rot	Total number	Number with neck rot
White Portugal	Topped	21	19	20	0
Do	Untopped	19	3	20	0
Yellow Globe	Topped	10	8	10	0
Do	Untopped	10	1	10	0
Red Globe	Topped	10	8	10	0
Do	Untopped	10	0	10	0

It is evident here, as with *Botrytis allii*, that the removal of the top and exposure of the wounded succulent tissue favors infection. In this instance a few more bulbs with tops intact were infected than was the case with *B. allii*. The difference is not great enough, however, to warrant the conclusion that *B. byssoidea* is more aggressive as an invader through the uninjured neck tissue, although this question deserves further study.

It is to be expected that inception of the neck-rot diseases in the field may be influenced by the condition of the neck tissues of the bulb when it is exposed to the parasites under favorable environment. In the experiments just described the bulbs were not exposed to the organisms until the tops were entirely mature. In the light of this evidence it might be expected that bulbs which were thoroughly mature before being subjected to the organisms would remain reasonably free from infection. The opportunity for prompt and thorough desiccation of the neck tissues does not always prevail in the field. In general those conditions which favor sporulation of *Botrytis allii* and *B. byssoidea* and subsequent germination of conidia are the ones which inhibit rapid curing of the onion tops. It remained for actual field experimentation to determine whether or not the best natural curing of bulbs with the tops left intact was sufficient to ward off infection by the neck-rot fungi.

FIELD DATA

The field studies were carried on in the onion-growing section of eastern Racine County, Wis. An area was selected where the crop had been grown repeatedly for many years and where mycelial neck rot commonly occurs on the stored crop. Unfortunately for this study, the gray-mold neck rot occurs only rarely in this section. The small sclerotial neck rot sometimes occurs, but it is confined to the white varieties, and they are grown to a very limited extent in this section. The field observations are therefore confined almost entirely to *Botrytis byssoidea.*

The first series of experiments was planned to compare the amounts of neck rot which developed in bulbs with mature and with immature necks at harvest. It was necessary to harvest such bulbs from practically the same spot and to handle them in the same manner in order to give equal exposure to natural inoculum and environing influences. Consequently a portion of a field was selected in which the crop was approaching maturity and in which the plants were ripening somewhat unevenly. The bulbs were harvested and divided into two groups designated as "mature" and "immature" according to the succulence of the neck tissues. They were then topped and placed in slatted crates, where they were allowed to cure in the open for some weeks, after which they were stored in an onion warehouse. The data obtained at the end of the storage periods are given in Table 8.

TABLE 8.—*Relation of maturity of neck tissue to natural infection of Red Globe onions by Botrytis byssoidea*

Year	Immature		Mature	
	Total number of bulbs	Percentage with neck rot	Total number of bulbs	Percentage with neck rot
1917	600	6.5	600	2.8
1918	363	21.2	661	8.6

Although the percentage of infected bulbs in the mature lots was small in both years, the amount was at least doubled in each case in the immature lots. These results are in line with what might be expected from the foregoing laboratory data.

The next matter of importance was to determine whether leaving the tops intact after harvest is a reliable barrier against infection. The possibility that it is, is suggested by the laboratory experiments, inasmuch as clipping the tops while only partially mature exposes the succulent wounds to natural inoculum. It is quite possible, however, that the fungus may become established in the dying tops before they are completely desiccated and thus gain ready access to the scales. Field experiments over a period of four years give a fair index as to the bearing of this point of natural infection. In each season from 1917 to 1920, inclusive, several bushels from the same area were harvested with and without tops. They were handled otherwise like the commercial crop. In 1917 and 1918 Red Globe variety was used. In 1919 White Globe and Red Globe varieties were used, but no neck rot developed in either lot; hence no report is included in the table. In 1920 Red, White, and Yellow Globe were used. In the last season two harvests were made. The first was on September 6, when the tops were not quite mature; the second was on October 9, some three weeks after harvest would normally occur, during which time they were exposed to some rainy weather. The percentage of neck-rotted bulbs was determined at the end of the storage period, and the data are recorded in Table 9.

TABLE 9.—*The effect of the removal of onion tops upon infection by Botrytis byssoidea; experiments at Racine, Wis., 1917–1920; data at end of the storage period*

Year and variety	Topped bulbs		Untopped bulbs	
	Total number	Percentage with neck rot	Total number	Percentage with neck rot
1917:				
Red Globe	1,228	5.1	1,164	0.6
1918:				
Red Globe	292	8.2	292	2.7
1920 (harvest on Sept. 6):				
Red Globe	243	0.0	194	0.0
Yellow Globe	224	0.0	214	0.0
White Globe	266	40.2	340	37.3
1920 (harvest of Oct. 9):				
Red Globe	340	0.2	365	0.0
Yellow Globe	323	5.5	297	0.0
White Globe	338	55.6	304	51.9

The data show the striking difference in susceptibility between colored and white varieties, a matter which will be discussed later. It is evident also that the bulbs in the earlier harvest, even though the tops were not quite mature at the time of harvesting, acquired less neck rot than did those which were harvested later, when the tops were mature. This is contradictory to the data previously discussed, in which mature and immature plants harvested at the same time showed the opposite results as to amount of infection. The bulbs harvested in early September had the advantage of good curing weather, which is also unfavorable for production of Botrytis conidia and infection. Those bulbs which remained longer in the field were exposed to environmental conditions more conducive to neck-rot infection. This is evidence therefore that the weather conditions are quite as important as the degree of maturity. Considering the effect of the removal of tops, it is evident that the bulbs of the white variety with tops left intact were affected nearly as severely as those which were topped. In the laboratory experiments (experiments 1, 2, and 3) the neck tissue of the bulbs was quite thoroughly desiccated before it was exposed to the organism. In the field this is not necessarily the case, and the difference in the field and laboratory results can only be explained by the supposition that infection in the field took place before the tops were completely cured. It is further evident that the harvesting of bulbs with the tops intact can not be relied upon as an effective means of control with the white varieties.

VARIETAL RESISTANCE

The fact has become well-established among onion growers and dealers that, of the varieties which are commonly grown for storage, the colored-bulb types have much better keeping qualities than the white-bulb type. The degree of susceptibility of the different varieties to the three neck-rot decays also tends to substantiate this fact. Munn (*20*) points out this difference in varietal susceptibility to *Botrytis allii*. In the Middle West it has been repeatedly observed in connection with *B. byssoidea*, and the results of a critical comparison are given in Table 9. Up to the present, *B. squamosa* has been found in nature only upon white bulbs or (in one instance) on bulbs having a very slight yellowish color. The high resistance of yellow and red bulbs is shown by the fact that in several cases where the small sclerotial neck rot occurred on white onions, colored bulbs grown next to them were completely free from the disease.

There is abundant evidence, however, that colored bulbs are not resistant once infection is established. In nature they are not always completely free from the gray-mold or mycelial neck rots. The difference between the amount of disease in colored and white varieties is usually striking, but such colored bulbs as become infected decay quite as readily as the white bulbs. Repeated comparative inoculations have been made with each of the three neck-rot organisms upon red, yellow, and white bulbs. The results have uniformly shown that infection by way of wounds in the succulent scales is attained quite as readily in one variety as in another, while the progress of decay following infection is approximately the same in colored and white bulbs inoculated with any one of the three forms of neck rot. Resistance in the colored bulbs appears to be due to the exclusion of the fungi. The outer scales and the neck tissue of pigmented bulbs contain a water-soluble substance which is decidedly toxic to the Botrytis forms as well as to certain other onion-bulb pathogenes. It has been suggested that this toxin may prevent the invasion of the neck tissue by the Botrytis organisms and thus preclude infection. Further details of this phase of the investigation have been presented earlier (*32*, *35*).[3]

CONTROL

The control of the neck rots of onion has not been completely worked out as yet. The wider use of colored varieties has served to reduce the losses in a considerable measure. The greatest hazard is encountered when the white varieties are grown. There is little in the way of crop rotation and sanitation with an intensively produced crop like the onion which can be relied upon to reduce the disease in environments favorable to it. The most hopeful measure so far devised is that of artificial curing of the bulbs after harvest to check the organisms in severely infected lots. The investigations, which so far have dealt primarily with mycelial neck rot, show that rapid desiccation of the neck tissues, even though infection has already become evident, will to a great extent prevent further advance of the disease. Preliminary results have already been published (*33*), and further experimental work is under way.

SUMMARY

Three closely related but distinct neck-rot diseases of onion bulbs have been described. They are distinguished as follows: Gray-mold neck rot (*Botrytis allii* Munn), mycelial neck rot (*B. byssoidea* Walker), and small sclerotial neck rot (*B. squamosa* Walker).

The symptoms of each disease have been described and the morphology and pathogenicity of each organism discussed.

The three organisms are readily distinguished by the character of their growth upon potato-dextrose agar.

[3] In the papers cited *Botrytis byssoidea* is referred to as *Botrytis* sp. 110 and *B. squamosa* is referred to as *Botrytis* sp. 108a.

All three organisms will produce growth on potato-dextrose agar over a range of 3° to 33° C., with most profuse development from about 20° to 25°. Spore germination occurs over a range of 3° to 27° but most promptly from about 19° to 27°. *Botrytis allii* and *B. byssoidea* sporulate at temperatures from 4° to 25° or higher, but *B. squamosa* seldom produces spores at temperatures above 20°. Infection and decay of the bulbs, however, are clearly favored most by temperatures below 20° and above 15°.

Field observations in the Middle West over a period of years show that *B. byssoidea* at least has been most prevalent during seasons in which the temperature was, on an average, below normal and the rainfall above normal.

Infection by *Botrytis allii* and *B. byssoidea* takes place more readily when the neck tissue is succulent at the time of exposure than when it has become desiccated. When harvested under comparable conditions, bulbs with immature tops showed a higher percentage of infection by *B. byssoidea* than did bulbs with mature tops. The removal of tops at harvest predisposes the bulbs somewhat more to infection by *B. byssoidea.* The difference between results with topping the bulbs and harvesting them with tops intact is not great enough, however, to warrant recommendation of the latter procedure as a means of control.

Colored varieties are in general less subject to attack by these three neck-rot organisms than are white varieties. When infection once occurs, however, decay proceeds with equal rapidity in both types. It is suggested that the water-soluble toxin present in the dry outer scales and neck tissue of colored bulbs aids materially in excluding the organisms.

The disease may be controlled in a large measure by the use of colored varieties. Artificial curing of the bulbs after harvesting so as rapidly to desiccate the neck tissues is also effective in checking the disease.

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